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Disruption of territorial behaviour in badgers *Meles meles*

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Badgers *(Meles meles)* typically live in mixed-sex social groups which defend permanent, communal and mutually exclusive territories (e.g. Kruuk 1978, 1989; Roper et al. 1986). Here we describe an unusual case in which a well-established and stable territorial system, involving several groups of badgers, was disrupted following the traumatic deaths of all the male members of one of the constituent social groups. The study was part of a longer-term investigation of badger behaviour and ecology in the South Downs, East Sussex, U.K. (for details of the study area and methods see Roper et al. 1986; Shepherdson 1986).

The data were collected between April 1986 and April 1988, and concern five neighbouring groups of badgers. From April to June 1986, group 1 consisted of five adult males, two females and one cub, of which four males were radio-collared and had been intensively radio-tracked. During the period June 21 to July 1 1986, all five males and the cub died, probably as a result of poisoning although post-mortem examination failed to confirm this. Following this incident, the two remaining females from group 1 (termed 1.1 and 1.2) were radio-collared on July 7, together with one male from each of groups 2 and 3 (2.1 and 3.1 respectively) and one male and two females from group 4 (4.1, 4.2 and 4.3 respectively). These animals were observed until October 1986, for at least 25 h per animal per month. In addition, bait-marking (Kruuk 1978) was carried out in April each year from 1984 to 1988, and in October 1986, on all 5 social groups. Badgers mark their territory boundaries by defecating at latrines (Roper et al. 1986), and the purpose of bait-marking was to allow territory boundaries to be mapped by determining which latrines were used by the members of each social group.

Bait-marking of setts 1–5, prior to the deaths of the group 1 males, showed the pattern typical of established territories in areas of high badger population density. Each main sett was surrounded by a network of latrines, such that the latrine systems of different setts defined contiguous and almost non-overlapping territories (Fig. 1a). By October 1986, however, three months after the death of the group 1 males, substantial overlap had appeared between territories 1 and 2 (Fig. 1b). At the same time, the whole of the area to the north-east of sett 1 was apparently no longer defended. By April 1987 (Fig. 1c), territories 1, 2 and 3 all overlapped considerably, to such an extent that territories 2 and 3 both encompassed the group 1 sett. A year later, however, in April 1988, the territorial situation had reverted to the original pattern, with territories 1–3 showing little overlap and their boundaries being more or less where they had been prior to the deaths of the group 1 males. The territories of groups 4 and 5 did not change subsequent to the deaths of the group 1 males, despite the fact that these territories were contiguous with that of group 1 and included latrines previously visited by members of group 1 (see Fig. 1a).

During the 2 years prior to the deaths of the males, members of group 1 never ventured more than 250 m into an adjacent territory and spent, on average, only 4.9 % of active time

outside their own territory. This is typical for our study area, where population density of badgers is high (about 12 adults/km^2) and territories are small (Shepherdson 1986). Following the deaths of the group 1 males, however, the two remaining females almost immediately began to travel far into, and sometimes beyond, adjacent territories (Fig. 2a). Female 1.1 was first seen entering territory 5 on July 9th 1986, when she spent over an hour feeding there. During the following months she repeatedly travelled into or beyond territory 5, often feeding up to 1 km away from her original territory. In September and October she began regularly to enter territory 2, though occasional visits to territory 5 continued. Female 1.2 regularly ranged over large parts of territory 2 during the whole of the period July–October 1986, though she too occasionally visited territory 5. Both females repeatedly visited

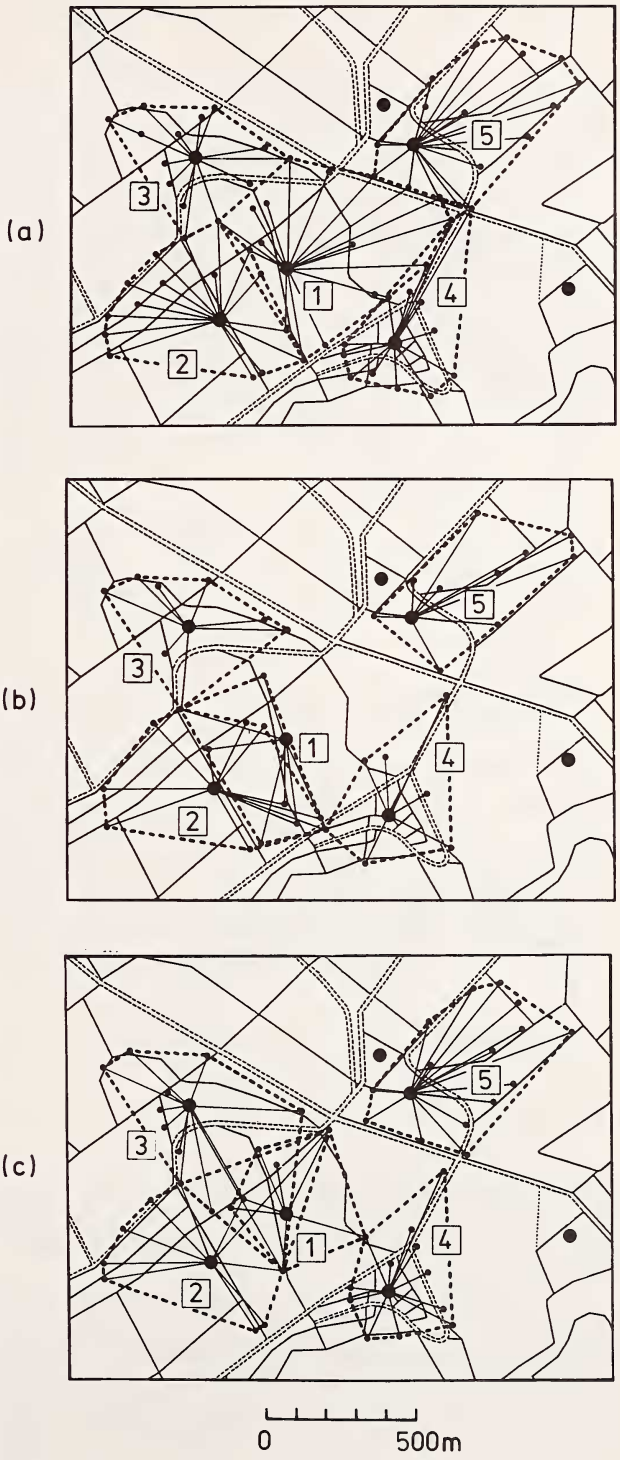

Fig. 1. Bait-marking maps showing territory boundaries (bold dashed lines) in (a) April 1984–1986 (data combined over all three years), (b) October 1986 and (c) April 1987. Territories are numbered 1 to 5. Large dots denote main setts, small dots denote latrines where bait-markers were found. Radial lines connect latrines where bait-markers were found to the main sett where the markers in question originated

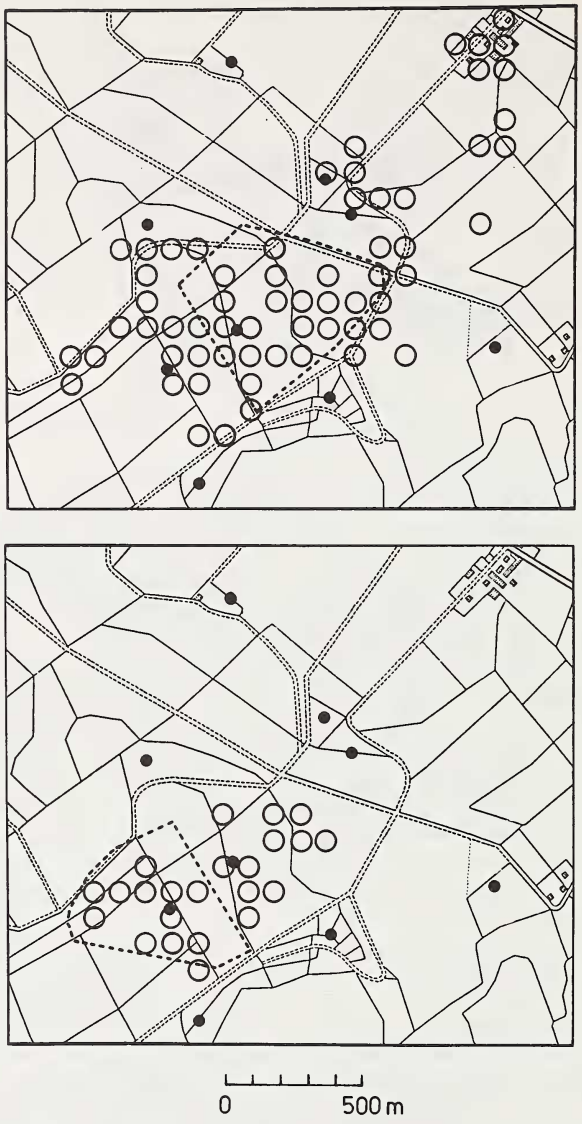

Fig. 2. Home ranges of (a) females 1.1 and 1.2 (data combined for both animals) and (b) male 2.1, during July–October 1986. The study area was divided into 0.25-ha grid squares (not shown), and open circles denote squares where the animals in question foraged. Filled circles show main setts; bold dashed lines show the original territory boundary, as determined by bait-marking, of (a) group 1 and (b) group 2

setts 2 and 5 and both were often seen feeding close to uncollared animals presumed to be members of groups 2 and 5: but no hostile interactions were observed.

From July 11 onwards, uncollared animals from neighbouring groups were repeatedly seen at sett 1 and elsewhere in territory 1, often in the company of one or other of the group 1 females. Male 2.1 ranged widely over territory 1 and regularly visited sett 1 (Fig. 2b). He also, on several occasions, foraged close to the group 1 females, either in his own territory or in theirs. Males 3.1 and 4.1, which were observed during the period July–October, also entered territory 1 on many occasions. Altogether, following the death of the group 1 males, females 1.1 and 1.2 spent 32 % and 25 % of their active time respectively outside the boundaries of their original territory, while for males 2.1, 3.1 and 4.1 the corresponding figures were 32 %, 28 % and 22 % respectively.

It is generally assumed that the primary purpose of territory defence in badgers is to monopolise food resources and that defence costs are shared by all members of a social group (see reviews by Kruuk 1989; Woodroffe and Macdonald 1993). However, it has also been suggested that territory defence is primarily a male activity and that its primary function is to deter neighbouring males from entering the territory for mating purposes (Roper et al. 1986). The dramatic changes in territorial and ranging behaviour that we

observed are, we believe, more readily explained by the mate-defence than by the food-defence hypothesis.

First, the group 1 territory rapidly decreased in size after the deaths of the resident males, and attempts to take it over were made by neighbouring groups, despite the fact that it was still inhabited by two females. Furthermore, the only neighbouring animals seen frequently to enter what was left of the group 1 territory were males. These observations suggest that males are more active than females both in territory defence and territory acquisition, and that resident males are the major deterrent to takeovers by adjacent groups (see also Kruuk 1978, 1989). Second, bait-marking showed that neighbouring groups only attempted to overlap parts of the original group 1 territory that were still being marked by the two females: no attempt was made to take over a large part of the group 1 territory that had apparently been vacated. This suggests that when neighbouring groups tried to expand their territories they were attempting to incorporate areas containing unguarded females, not to incorporate unused foraging areas. Third, the two group 1 females were repeatedly seen foraging in neighbouring territories, close to inhabitants of those territories, yet no aggressive interactions were seen. This suggests that territory holders are not primarily intent on monopolising food resources.

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